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A SURVEY OF THE HAWAIIAN LAND FLORA

VAUGHAN MACCAUGHEY

(WITH FIVE FIGURES)

The Hawaiian Archipelago has long been known to the scientific world as a peculiarly isolated island world with many extraordinary biological features. The remoteness of the group from continental areas, the exclusively volcanic nature of the mountains, the extreme specialization of many plant and animal forms—these and many other unique conditions have given particular interest to the biological problems of Hawaii (fig. 1).

It is the purpose of this paper to make a rapid survey of the prominent characteristics and elements of the Hawaiian land flora.¹ The timeliness of such a survey is evident to all who have followed the researches of recent years in the various departments of natural science, as these studies have in many instances necessitated extensive revision of previous records. In order to compress the material within reasonable bounds, much interesting detail is necessarily omitted, and numerous problems of great interest from the standpoint of philosophical biology² can here be accorded only passing mention.

¹ For purposes of convenience all of the algae and fungi except the conspicuous woody and fleshy forms are excluded from this consideration of the land flora.

² Undoubtedly, after the systematic work on the various groups comprising the Hawaiian fauna and flora has been brought to a stage of comparative completeness, the greatest contributions will be made in the field of philosophical biology. Some of these contributions are suggested in the sections on endemism and precinctiveness in this paper.

For an account of the physical aspects of the Hawaiian Islands, their topography, climate, volcanoes, soils, and geological history, all of which have important and complicated relations with the flora, the reader is referred to such standard treatises as BALDWIN'S *Geography of the Hawaiian Islands*, BRYAN'S *Natural history of Hawaii*, HITCHCOCK'S *Volcanoes of the Hawaiian Islands*, and the excellent article on Hawaii in the latest edition of the *Encyclopedia Britannica*.



FIG. 1.—Map of the larger islands of the Hawaiian Archipelago

Endemism

A few quantitative statements will elucidate the remarkable endemism of the Hawaiian land flora. There are approximately 1200 species of native plants, exclusive of algae, fungi, and bryophytes. This is also exclusive of the 25, more or less, brought in by the primitive Hawaiians, and discussed later in this paper. Of this number about 200 have been introduced and established within historic times, leaving about 1000 genuine indigenous species. Approximately 700 of these are endemic, thus constituting 70 per cent of the vascular land flora. Restricting the

calculation to "flowering" plants alone, it is estimated that *more than 85 per cent* are endemic. This is a proportion unequaled in the annals of geographical botany. It is particularly significant when compared with the 34 per cent of Samoa, 35 per cent of Tahiti, and 53 per cent of Fiji.

New Zealand, with a land area of 100,000 sq. m., 16 times that of Hawaii, has no more species of flowering plants than Hawaii, and its percentage of endemism, about 75, is markedly lower. Japan, with a total area of 175,000 sq. m., some 28 times that of the Hawaiian Archipelago, has but 1500 species of flowering plants, only 300 more than Hawaii. There is no other region on the earth, of similar area, with so large a list of endemic forms as Hawaii.³

In addition to the native flora proper, there are probably 1000 additional species in cultivation or semicultivation in the plantations, ranches,⁴ gardens, nurseries, and fern and orchid houses of Hawaii. These have been gathered from all parts of the world, with a natural emphasis upon tropical and subtropical species.

The lucid and comprehensive statement of PERKINS, the eminent student of Hawaiian zoology, is pertinent at this point.

A comparative study of the many groups of animals represented in the islands, and of the affinities of species to species, and genus to genus, in the groups of allied forms, has led me to believe in the extreme rarity of a successful immigration from outside. The extraordinary gaps in the fauna of whole families of wide distribution, and containing countless species, many of which no doubt would, and some of which after introduction by man are known to thrive in the islands, show clearly how hardly and rarely have immigrants reached them from outside. A limited number of birds and insects, species of well known migratory habits, for which no seas are impassable, doubtless arrive continuously, but these, only in the event of such migration ceasing, are likely to produce new and endemic forms.

The phenomena exhibited by the flora appear to me to be extremely similar to those of the fauna. There may be seen the same notable absences

³ See LYDGATE, The endemic character of the Hawaiian flora. Thrum's Hawaiian Annual. 1911 (pp. 53-58).

⁴ Extensive areas on Hawaii, Maui, and Molokai, for example, aggregating hundreds of square miles, are overrun with introduced ranch grasses. These form a dense continuous sod, which not only drives out the native grasses and herbs, but also prevents the germination of seeds of the forest trees and other native plants.

of forms widely distributed elsewhere, the same multiplication of allied species of many of the genera that are present, the same groups of allied genera, embracing many species. I believe that the explanation of these facts is quite in accordance with that which I think to be true of the fauna, as above stated. . . . The present Hawaiian fauna is derived from waifs and strays from all directions. At rare intervals from the Eocene till now chance immigrants have arrived. Some have been able to establish themselves, many more probably, even after a landing had been effected, have failed. Those that have been successful and have found congenial conditions have often thriven amazingly, giving rise to hosts of descendant species, as they have become adapted to or become modified by diverse conditions. . . . Where conditions have proved favorable and remained so, and plant or animal has become adapted to special conditions, an exuberance of distinct forms has sprung from the ancient immigrant. Such cases are manifest in the Lobeliaceae amongst plants, and in many groups of animals, the Drepanididae (birds), Plagithmysidae (insects), Achatinellidae (mollusca), and many others. Such form the chief and most interesting part of the native fauna and flora of the present day.⁵

Precinctivity

A second notable feature of the flora is the highly precinctive ranges of many species and varieties. This sharply defined localization of habitat has reached a very advanced stage with many forms. The condition is closely analogous to the equally remarkable precinctive distribution of the arboreal snails (Achatinellidae), and many of the native birds and insects, and is undoubtedly due to the same environmental and evolutionary factors.

The statement may be made conservatively that a very large percentage of the endemic Hawaiian plants are closely confined within areas of a few square miles, and in many instances of a few square rods.⁶ Thorough botanical explorations of the past few

⁵ From PERKINS' introduction to the *Fauna Hawaiiensis*, being the land fauna of the Hawaiian Islands; by various authors; published in 6 parts, 1899-1913. Cambridge University Press. It may be remarked that endemism is strongly exhibited among the Hawaiian lizards, crabs, holothurians, madreporarians, and various marine groups. See also GULICK, JOHN T., *Evolution, racial and habitudinal*. Carnegie Inst. Washington. 1905, especially pp. 1-5, dealing with endemism of Hawaiian land shells.

⁶ MACCAUGHEY, V., *Precinctive flora of the Waianae Mountains*. Hawaiian Forester 13:85-89. 1916; and *Gunnera petaloidea* Gaud. Amer. Jour. Bot. 4:33-39. 1917.

years have failed to disclose new habitats or localities for many of these precinctive plants. For example, *Drosera longifolia* occurs only in the summit bogs of Kauai; *Pelea pallida* is limited to Kaala, in the Waianae Range; many of the lobelias, cyrtandras, and kaduas are sharply precinctive; *Lagenophora mauiensis* occurs only in the Eeka swamps; and 40 or 50 other well defined illustrations might be cited.⁷

The limitations of this paper forbid any extensive discussion of the remarkable geological history of the Hawaiian Archipelago, and the bearing of this history upon the development of the land flora.⁸ It is sufficient to state that the older islands lie to the westward, and that the eastern end of the chain comprises the youngest elements of the group. Many years ago HILLEBRAND noted the contrast between the vegetation of Kauai and Mauna Loa as two extremes. He stated that "the Kauai species of the leading Hawaiian genera are in all instances the most specialized, to be distinguished by more striking characters than the others. Examples are *Schiedea*, *Raillardia*, *Dubautia*, *Campylotheca*, *Lipochaeta*, *Pittosporum*, and *Pelea*. The proportion of species peculiar to Kauai with species peculiar to all the other islands is about 67:382, or 17.5:100."

The studies and explorations of succeeding botanists have tended to confirm and intensify this contrast. Kauai, Waianae on Oahu, the east end of Molokai, West Maui, Kohala and Puu Waa-waa on Hawaii, these are regions much more ancient than the land areas with which they are immediately connected, and their vegetation gives abundant evidence of their antiquity. During the summer of 1916 Professor W. A. BRYAN, of the college of Hawaii, made explorations on the summits of the high mountains of Hawaii which gave abundant and conclusive evidence of a former period of glaciation. His notable discoveries add to the

⁷ MACCAUGHEY, V., Vegetation of the Hawaiian summit bogs. Amer. Bot. 22: 45-52. 1916.

⁸ The geological researches of recent years have demonstrated that the islands are by no means simple in structure, as was once believed, but on the contrary show innumerable evidences of prolonged and profound geological changes. The complexity of these changes has only lately been fully appreciated, and their unraveling will require painstaking research for many years to come.

accumulating data which point to the great antiquity of this archipelago and to its complex geological history.

Extinction

The flora of today strikingly illustrates the profound biological changes concomitant with the coming of foreigners⁹ and the spread of their industries. Practically all of the arable lowlands have been converted into plantations, and are covered with sugar cane, pineapples, and other crops. The level uplands have become sheep and cattle ranches. Agriculture has wiped out practically all the native vegetation in all of these utilizable regions, and the indigenous flora is now largely confined to the mountains and the waste lands.

Feral and semi-wild goats, sheep, swine, and cattle have been the most serious and persistent foes of the native flora. For over a century they have roamed almost unchecked through the forests, overrunning the mountainous districts, and in some instances whole islands. They have totally destroyed or irreparably damaged untold quantities of indigenous vegetation. Many districts have been stripped of all save the weediest and least edible of plants. Some of the smaller islands (Niihau, Lanai, and Kahoolawe) that have long been overstocked with these herbivorous vandals have been depleted almost wholly of the original native flora. The destruction of the vegetative protective covering has exposed these regions to the full force of erosion by wind and water, and this has resulted in the removal of huge quantities of surface soil.

It is difficult to conceive the transformations wrought in the Hawaiian forests by man¹⁰ and his live stock, so extensive have been the devastations. Many herbaceous species have undoubtedly been totally exterminated. Some of the woody species that have become extinct within historic times, or are now on the verge of

⁹ Foreigners, that is, others than native Hawaiians; especially Americans, British, Germans, etc.

¹⁰ In the early days the woodlands in the vicinity of the numerous sugar mills and plantations were cut to supply fuel for the mills, and for the plantation villages. The latter use continues to the present time, and there is a serious shortage of firewood on all the islands.

extinction, are *Neowawraea phyllanthoides*, *Alectryon macrococcus*, *Alphitonia excelsa*, *Hibiscadelphus Giffordianus*, *H. Wilderianus*, *H. hualaliensis*, *Kokia Rockii*, *K. drynarioides*, *Clermontia haleakalensis*, *Cyanea arborea*, *C. comata*, and *Hesperomannia arborescens*.

It may be estimated conservatively that probably several hundred species of angiosperms have become extinct since the first landing of live stock on these islands. PERKINS has estimated that 300 species of native insects have been exterminated. The extinction of many of the highly specialized avian species is a lamentable and widely known fact. On the island of Oahu, for example, there are more extinct species of endemic birds than existing species. Numerous forms of the arboreal snails are now excessively rare.

Ocean currents

Hawaii is so remote from other land areas, and is so situated with reference to the great trans-Pacific ocean currents, that comparatively few plants have been added to her flora through the agency of water borne seeds. The shores and beaches present a striking contrast to the forested littoral of many South Pacific Islands, which have been well stocked with plants by the currents.¹¹

Logs of coniferous species are thrown upon Hawaii's windward shores after a long drift from the northwest coast of America. These have probably brought seeds and spores in their crevices, although there is no conclusive evidence on this point.¹² BRYAN'S hypothesis is very suggestive in this connection. "It is possible that in bygone ages, long ago, the movements of the Pacific may have been reversed, so that various plants from the Australian, Polynesian, and South American regions that are well known here, might have been carried to the islands by them, in one way or another."

Some of the species that very probably have been introduced by ocean currents are *Scaevola Lobelia*, *Heliotropum curassavicum*,

¹¹ Seeds of the following woody species are common in the drift material along the beaches: *Aleurites moluccana*, *Calophyllum Inophyllum*, *Terminalia Catappa*, *Mangifera indica*, *Cocos nucifera*, *Thespesia populnea*, *Pandanusodo ratissimus*.

¹² See WARMING, E., *Botany of the Faroes*. Copenhagen. 1903 (Vol. 2, pp. 660-681; particularly pp. 674-678, on plant immigration across the sea).

H. anomalum, *Vitex trifolia*, *Ipomoea pes-caprae*, *I. acetosaefolia*, *I. bona-nox*, *I. tuberculata*, *Vigna lutea*, *Mucuna gigantea*, *Batis maritima*, *Sesbania tomentosa*, *Capparis sandwichiana*, *Erythrina monosperma*, *Ruppia maritima*, *Colubrina asiatica*, *Dioclea violacea*, *Strongylodon lucidum*, *Caesalpinia Bonducella*, *Cassytha filiformis*, and numerous grasses and sedges.

HITCHCOCK cites *Pandanus* as a typical current disseminated plant.

A good illustration of the origin of the vegetation is the screw pine, *Pandanus*, or lau hala. . . . These seeds will stand saturation in water for months without losing their vitality. Hence they may be carried hundreds or thousands of miles from the place of their nativity, and when washed inland by unusually high waves will be placed where they will sprout and grow up. I once saw a place in Kauai where hundreds of young lau halas had started to grow near the seashore. . . . There is no tree with wider range in the Pacific than the *Pandanus*. And it was in existence in the Triassic period in Europe. It is therefore one of the oldest and most persistent of plants, and the one best fitted to start plant life on the isolated volcanic islands for the first time peering above the waves.¹³

Duration of migration

The philosophical presentation of the status of Hawaiian plant immigrants with reference to the evolution of endemic forms has been made so comprehensively by PERKINS that an extract from his statement is given here.

Although endemicity of plant or insect, as represented by great peculiarity of structure and usually by the occurrence of numbers of allied species, naturally indicates a very ancient occupation of the land by their immigrant ancestors, yet it does not necessarily follow that paucity of species or the apodemicity of a genus denotes a comparatively recent immigration. A classification of the flora, as belonging to a definite age or era, based on such a supposition will certainly prove erroneous. It is not probable that all immigrants that arrive and become established are able, even after vast time, to become adapted to such diverse conditions as others, and some doubtless are much more slow to do so than others.

The evolution of new genera or species would proceed in a very different manner in different cases. In judging the length of time that any particular

¹³ It is quite possible that the *Pandanus* was first brought to the islands by the ancient Hawaiians, from their home in the South Pacific, where this tree is abundant; see concluding section of this paper. Also see GATES, F. C., The pioneer vegetation of Taal Volcano. *Philippine Jour. Sci.* 9:391-434. pls. 8. 1914.

plant or group of allied plants has existed in the islands, the botanist would be well advised to consider the fauna that is especially attached to these. When one considers that trees little modified from foreign species, for example, *Acacia koa* or *Sophora chrysophylla*, possess a great endemic fauna, not only species, but even genera of birds and insects, quite restricted to or dependent on them, and that some of these creatures are certainly themselves not less remarkable in their peculiarities than the most peculiar of the composites or lobelias, we may hesitate to attribute such plants to a later era than many other elements of the flora, which at first sight appear far more ancient.

Again, while in the islands an abundant endemic fauna restricted to a plant indicates an ancient occupation by the latter, the absence of such a fauna does not necessarily imply the reverse. In a fauna of comparatively few types it may happen that few or no species have reached the islands that could become adapted to certain elements even after great length of time. I think that those who are in favor of the comparatively frequent accession of immigrants to account for the great series of allied species, or groups of allied genera, hardly make full allowance for the great age of the islands. HITCHCOCK remarks in writing of the most recent portion of the group, the still active Mauna Loa on Hawaii, when one considers how little the bulk of the mountain is made up of the few flows delineated on the map, and how small a portion of the whole mass these can be, he is overwhelmed by the certainty that there were millions of streams and that millions of years must be assumed in order to say how old the mountain is. It must have commenced to build up long before the Tertiary period. And here he is considering the most recent portion of the group, and not the vastly more ancient parts.¹⁴

It is significant that the gymnosperms are entirely absent from the native Hawaiian flora; cycads and conifers have been introduced in recent years.

Zonation

In the Hawaiian Archipelago the large ecological zones are well defined. Elevation above sea level and precipitation are the two dominant factors which determine the local phytogeography. The zonal distribution of the endemic and indigenous vegetation is very pronounced; a very general statement may be made to the effect that the flora perceptibly changes in kinds and quantities of species with every 1000 feet of ascent (figs. 2-5). The following synopsis of the chief zones will serve to indicate the important phytogeographic areas:

¹⁴ See also SCHIMPER, A. F. W., Die Indo-Malayische Strandflora. Jena, 1891.

1. Littoral.—(a) *Humid littoral*, along the windward coasts; (b) *arid or semiarid*, along leeward coasts and coasts far removed from the mountainous interior.

2. Lowlands.—Up to 1000–1500 ft., with humid and arid sections, depending upon relation of topography to trade winds and distance from interior mountains.

3. Forest zone.—(a) *Lower forest* (1000–2000 ft.), with humid and arid sections; in early times this zone extended much farther seaward on the various islands than it does now; (b) *middle forest*



FIG. 2.—View from a dividing ridge between 2 long humid valleys, looking toward the head of Kau-kona-hua Valley; fog-covered summit ridge, elevation 2500 ft., seen in distance; entire region covered with dense and unbroken rain forest; on slopes and ridges trees average 15–30 ft. in height, in valley and ravines they rise to 40–60 ft.; annual precipitation at head of this valley approximates 200–300 inches.

(1800–5000 ft.), range variable, with humid and arid sections; this comprises in the humid areas the typical Hawaiian rain forest, highly hygrophytic and very rich in endemic forms; (c) *upper forest* (5000–9000 ft.), restricted to the high mountains of Maui and Hawaii.

4. Summit regions.—(a) *Xerophytic summits* (9000–14,000 ft.); high mountains of Maui and Hawaii; (b) *hygrophytic summits* (4000–6000 ft.); peaks rising into the cloud zone, with summit bogs.

Palms

The palms furnish an interesting illustration of the 3 floral elements: indigenous, native introductions, and modern introductions.¹⁵ The capital city, Honolulu, is a veritable palm garden; there are some 80 species represented, which have been gathered from all parts of the tropics. There is scarcely a home or yard without its palms; some of the finest driveways are colonnaded with such stately species as *Oreodoxa regia* and *Phoenix dactylifera*;

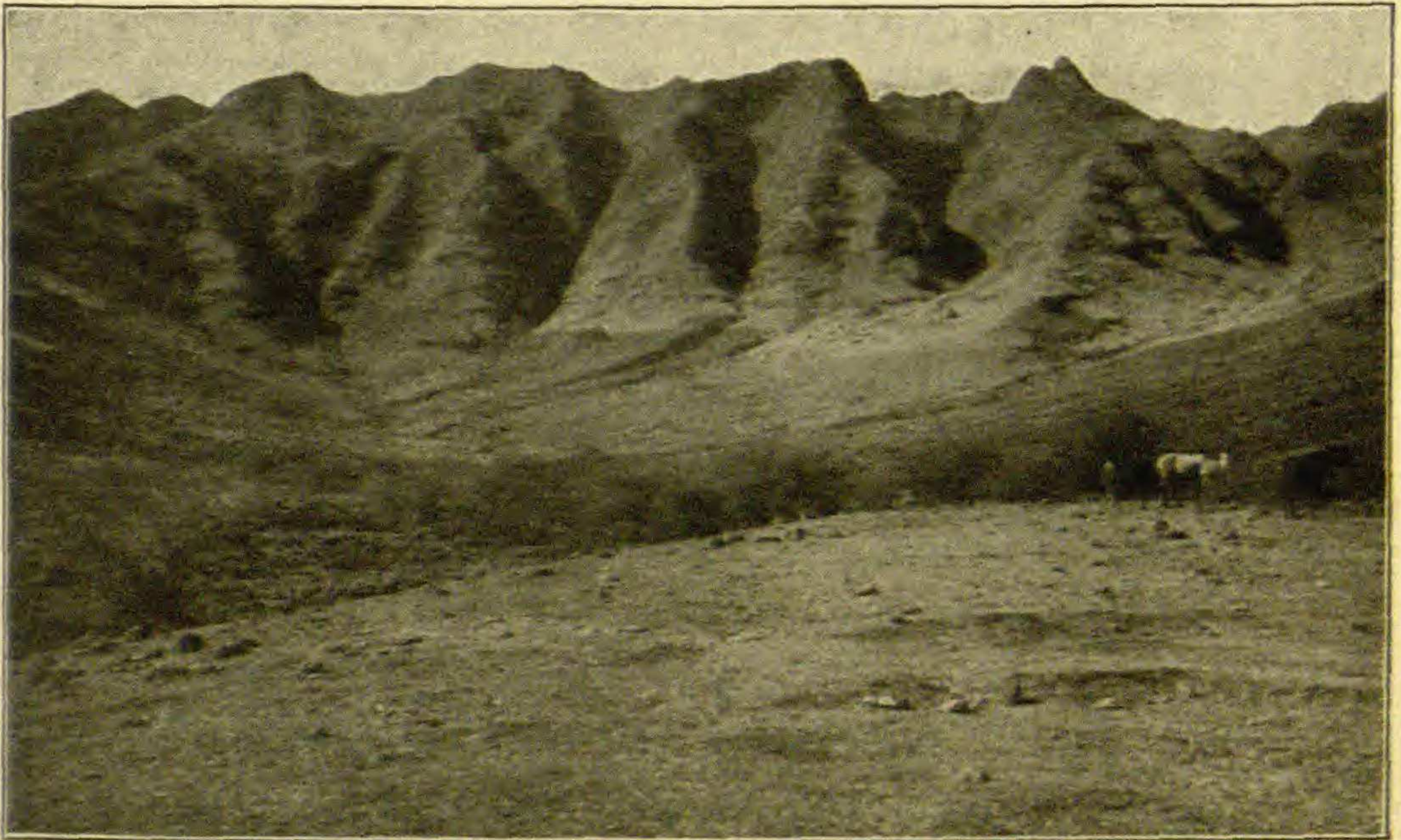


FIG. 3.—Arid, deeply eroded summit ridge, elevation 2000 ft., of eastern Koolau Mountains; absence of vegetation due partly to aridity, partly to devastations of goats; remnants of original forest cover occur here and there in hanging valleys near sky line and in deep ravines.

and certain of the old estates, the famous Hillebrand gardens for example, are crowded with rare and choice specimens. The only palm introduced by the natives (and this introduction is necessarily more or less theoretical, in the absence of historical records) was the coco palm. This species (*Cocos nucifera*) is widely spread throughout Polynesia, and in early times formed a characteristic feature of many Hawaiian shores and beaches.

¹⁵ MACCAUGHEY, V., The economic woods of Hawaii. *Forest Quarterly* 14: 696-716. 1916.

The indigenous palms are confined to the single genus *Pritchardia*, and are all endemic. There are a number of Hawaiian species, perhaps a dozen. The exact botanical status of these has not as yet been fully determined. The species of *Pritchardia* occur mainly in the rain forests and along exposed humid summit ridges. They are scattered, are usually solitary or in small clumps, never form pure stands, and constitute a very minor element in the forest. From the standpoint of abundance or striking features,

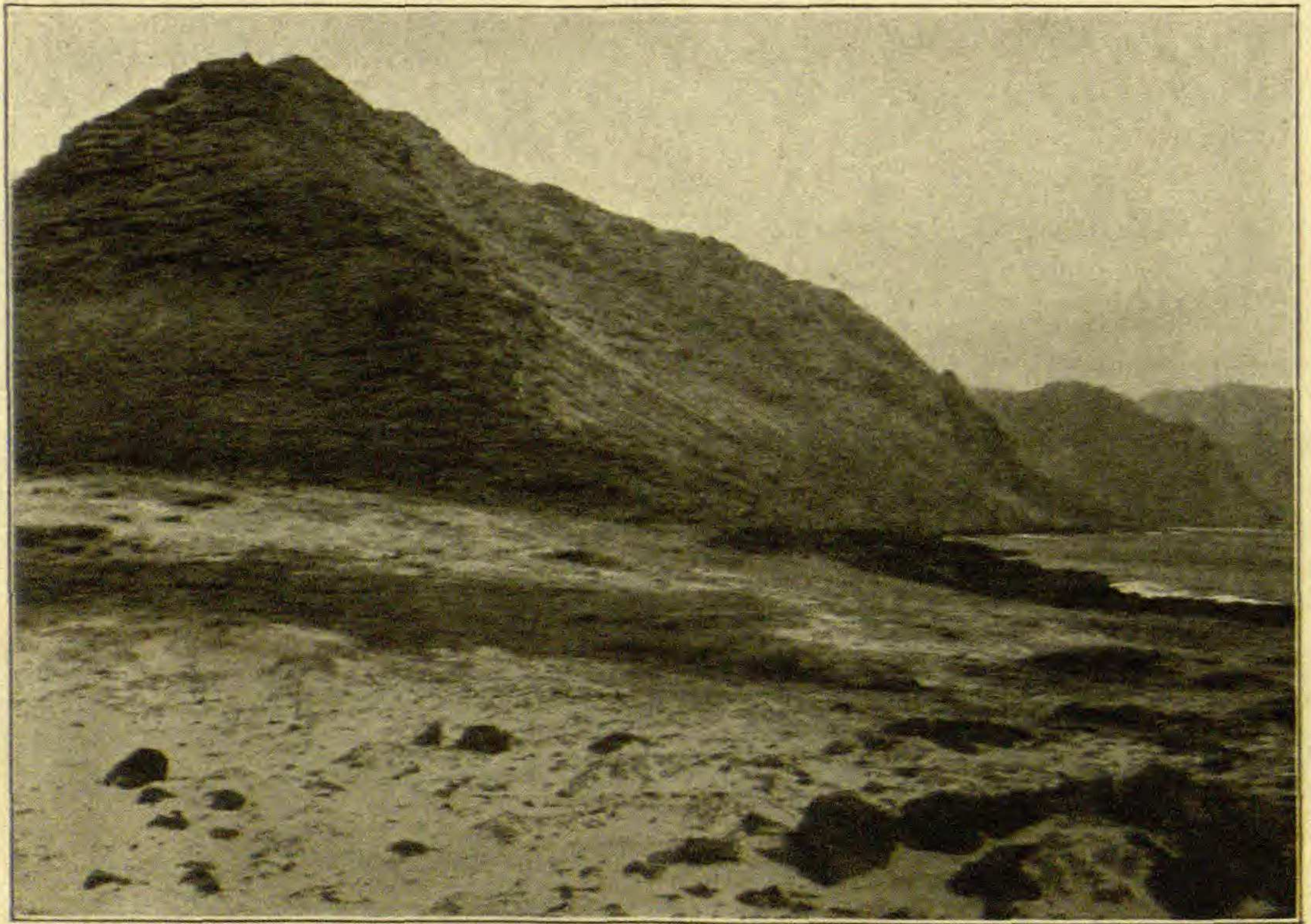


FIG. 4.—Xerophytic promontory, Ka-ena Point, a typical “dry ridge” formation; other similar ridges, separating arid valleys, seen to the right; in foreground a coral beach formation covering ancient lava beds; note stratification of lava flows in the faces of promontory, also extensive talus slopes.

the native palms are as disappointing as the native orchids. They occasionally attain considerable height (40–50 ft.), but are customarily of short or even dwarf stature. *Pritchardia* is confined to the islands of the Pacific. The Hawaiian species show close affinities with those of the South Seas.

Many of the other monocotyledonous families are but meagerly represented. The Orchidaceae, for example, that attain unrivaled

luxuriance and marvelous specialization in many tropical regions, have only 3 species in Hawaii, and these are all shy, poor, homely little plants.¹⁶ *Pandanus* is represented by one species, formerly abundant in the lowlands. *Freycinetia Arnotti* Gaud. is a tall woody liana, common in the lower forest zone of all the islands, and often forming dense jungles.

The liliaceous plants of Hawaii are in part woody species; none are bulbs, and none have particularly showy flowers. Of the



FIG. 5.—Lava flow of the smooth or "pa-hoe-hoe" type; shows invasion by lichens and ferns; in arid situations lava flows retain a new, fresh appearance for a long period of years; under humid conditions they rapidly disintegrate and are soon covered with plant life.

5 genera, 3 are monotypic: *Cordyline terminalis*, a tall shrub; *Dracaena aurea*, a tree; and *Dianella odorata*, a large herbaceous perennial; all are abundant. *Astelia* and *Smilax* are confined to the forest and upper zones, and none of the group occur on the coastal plains or lowlands. There are no "fields of lilies" in Hawaii. *Commelina nudiflora* is exceedingly abundant in moist

¹⁶ MACCAUGHEY, V., The orchids of Hawaii. *Plant World* 19:350-355. 1916.

situations throughout the lowlands, forming pure stands and smothering other vegetation.

The large and highly diversified tropical order of the aroids has no place in the Hawaiian flora, except 2 naturalized species, *Colocasia* and *Alocasia*, introduced by the ancient Hawaiians. *Colocasia antiquorum*, the kalo or taro, was the staple food of the primitive Hawaiians. The plant was raised both in irrigated fields (*loi*) and on the uplands (*Kula*). *Alocasia macrorrhiza*, the ape or giant taro, was raised in clearings in the lower forest, and used chiefly in time of famine. Ornamental aroids of many genera are now abundant in Honolulu gardens, but these are strictly exotic, and none of these are naturalized.

Another group that one naturally associates with a tropical background is the Begoniaceae, and yet of the 400 species, only one is native to the Hawaiian Archipelago. Our lone species is endemic, and is so distinct from its relatives that it has been placed in a monotypic genus, *Hillebrandia*. It is a beautiful plant with ornamental foliage and fine showy clusters of pink flowers, but is limited to such isolated and difficult regions that few people, either natives or whites, have seen it.

Lobelias

Unquestionably the crowning glory of our flora are the arborescent lobelias. These constitute one of the unique elements of the Hawaiian forest flora, and aggregate some 100 species, distributed among 6 genera, 5 of which are endemic. As ROCK¹⁷ succinctly states, "nowhere in the world does this tribe reach such a wonderful development in such a comparatively small area."

The lobelias surpass in number of species all other plant families comprising the Hawaiian land flora. Many of the species show extreme specialization. The extraordinary range of variation strongly suggests that we are witnessing the last spasmodic outbursts of the evolutionary impetus of this group. Quite unlike the small herbaceous lobelias familiar on the continent, all of our species have stout woody stems. The majority are tall shrubs or

¹⁷ ROCK, J. F., Synopsis of the Hawaiian flora. Thrum's Annual, Honolulu. 1912 (pp. 82-91).

trees, and some reach the amazing height of 40 ft. Many species have a slender, naked, palmlike trunk, closely marked with conspicuous leaf scars. This pole terminates in a large rosette of foliage and a showy inflorescence. These and other characters give the plant a deceptively primitive aspect.

The Hawaiian genera are *Brighamia*, endemic, 1 species; *Lobelia*, 5 endemic species; *Clermontia*, endemic, 17 species; *Rollandia*, endemic, 6 species; *Delissea*, endemic, 7 species; *Cyanea*, endemic, about 45 species. There are many features, both structural and ecological, which strongly suggest that our lobelias are the remnants of a very ancient flora, a flora that has well nigh been obliterated by profound geological and climatic changes.

It is significant to observe that the other islands of the Pacific are practically lacking in lobelias. Furthermore, in other parts of the world these plants are notably alpine in distribution. Many high mountains of the tropics and subtropics are marked by a lobeliaceous flora similar to that of our Hawaiian mountains. These and other facts in local phytogeography lean strongly toward the geological hypothesis that at one time these island mountains stood at a much higher level (perhaps thousands of feet higher) above the sea than at present. Under this theory the islands as they now stand are but the vestiges of a former extensive land mass.¹⁸ PILSBURY uses this hypothesis to explain the extraordinary geographic distribution of the Hawaiian arboreal mollusks. It undoubtedly has an application to such phytogeographic problems as are involved in any attempt to elucidate the origin of the Hawaiian lobelias.

Cyrtandras

One of the largest of the Hawaiian genera, and notably rich in endemic species and varieties, is *Cyrtandra*. The genus ranges throughout the islands of the Indian and Pacific oceans and in China, with a total of about 200 species. Of the 30 or more Hawaiian species, all are soft-wooded shrubs, and practically all are endemic. The remarkable variability of the genus is manifest

¹⁸ HILLEBRAND, WILLIAM, *Flora of the Hawaiian Islands*. 1888; published posthumously; out of print for many years; the standard flora of the islands, although now in serious need of taxonomic revision.

to a high degree by many of our species. As HILLEBRAND states, "the polymorphism of the Hawaiian cyrtandras is extraordinary; no single form extends over the whole group, and not many are common to more than one island. The variations affect every part of the plant, and branch out and intercross each other in manifold ways to such an extent that it is next to impossible to define exact limits of species."¹⁹ The evolutionary status of our species is closely analogous to that of the native lobelias.

The species of *Cyrtandra* are largely confined to the humid regions; they are precinctive and extremely shade-tolerant. Many species are to be found only in the narrow-walled ravines and dimly lighted recesses of the rain forest. *C. cordifolia* Gaud., *C. Pickeringii* Gray, *C. gracilis* Hbd., *C. Kahilii* Wawra, *C. grandiflora* Gaud., *C. paludosa* Gaud., *C. latebrosa* Hbd., and *C. Lessoniana* Gaud. are representative Hawaiian species of this genus.

Composites

Second only to the lobelias in importance are the Compositae. There are over 80 species, representing 29 genera; of these, 60 species are distributed among 9 endemic genera. Several of the genera (*Argyroxiphium*, *Wilkesia*, *Hesperomannia*, and *Remya*) show many evidences of isolated and specialized evolution and, as HILLEBRAND remarks, "probably belong to the oldest denizens of our islands, a supposition countenanced by the fact that each holds no more than two species." With reference to the last statement it must be remarked that several new forms in these groups, probably of specific rank, have recently been discovered.

A number of these peculiar Compositae (*Artemisia*, *Dubautia*, *Raillardia*) are arborescent, and alpine in habitat. On the high mountains of Maui and Hawaii they reach an elevation of 10,000 feet. *Lagenophora* is a peculiar summit bog form.

To this family belongs one of the most famous of Hawaiian plants, the beautiful silver sword (*Argyroxiphium sandwicense*). This plant has a large, compact basal head of dagger-shaped leaves

¹⁹ WINNE, W. K., Intercontinental land connections and their relations to plant migrations. Chicago. 1914 (p. 24, "The Pacific continent").

densely covered with shining silvery pubescence; from this body arises a tall inflorescence (6–8 ft.) of showy purple flowers. This unique herbaceous perennial is xerophytic, and occurs only at high elevations on Maui and Hawaii.

Lipochaeta, *Coreopsis*, and *Tetramolopium* are large genera of herbaceous or semiligneous perennials; there are 10 or 12 species in each genus, mostly endemic. The flowers are small, but very numerous, and form showy masses of rich yellow. *Bidens*, *Ageratum*, *Xanthium*, *Sonchus*, *Vernonia*, *Erigeron*, *Gnaphalium*, *Franseria*, *Eclipta*, and *Centaurea* are common weeds of the roadsides and fields.

Modern research in ornithology has demonstrated the existence of several bird migration routes from South America to the north via Hawaii. The Hawaiian goose and the Pacific golden plover furnish specific instances of these long over-sea migrations. Inasmuch as a number of the endemic composites show close affinity with certain Andean and other South American species, it is highly probable that they were carried thither by migrating birds.²⁰

A number of other native plants were probably brought by the same agencies, for example, *Rubus*, several endemic species, closely related to Pacific Coast forms; *Nertera depressa*, with fleshy red drupes, a South Pacific Coast species; *Fragaria chilensis*, which also occurs along Pacific America; *Dodonea viscosa*, with glutinous capsules, and widely dispersed; *Lycium sandwicense*, and others.

Leguminosae

The vast family Leguminosae, rivaled in size and distribution only by the Compositae, is abundantly represented in our flora. There are nearly 30 genera, many of comparatively recent introduction, but now well and widely established. Four genera, *Acacia*, *Sophora*, *Mezoneurum*, and *Erythrina*, are arborescent. Endemic species occur in *Vicia*, *Canavalia*, *Vigna*, *Acacia*, *Mezoneurum*, and *Sophora*. There are many introduced leguminous plants in Honolulu; particularly conspicuous are the flowering

²⁰ See ERNST, A., The new flora of the volcanic Island of Krakatan. Trans. by SEWARD. Cambridge. 1908 (pp. 58–60, "Seed-dispersal by birds").

trees of *Cassia*, *Poinciana*, *Peltophorum*, *Pithecolobium*, and allied genera.²¹

A number of the indigenous legumes are beautiful, high-climbing woodland vines, with showy clusters of bright colored flowers; *Syrongylodon lucidum*, *Vicia Menziesii*, *Mucuna urens*, *Dioclea violacea*, and *Canavalia galeata* are examples of these. Species of *Crotalaria*, *Indigofera*, *Leucaena*, *Acacia*, *Mimosa*, *Dolichos*, *Medicago*, *Phaseolus*, and *Desmodium* are common roadside weeds. The most valuable and widely known of our cabinet woods, *koa*, is from the common forest tree *Acacia koa*.

Rubiaceae

The Rubiaceae comprise a large and diversified portion of our flora. There are 13 genera, of which 4 (*Kadua*, *Gouldia*, *Bobea*, and *Straussia*) are endemic. There are between 50 and 60 rubiaceous species; of these the majority are tall shrubs or arborescent. The other genera (*Gardenia*, *Plectronia*, *Coffea*, *Morinda*, *Psychotria*, *Paederia*, *Nertera*, *Coprosma*, and *Richardsonia*) occur in many other tropical regions.

Of special interest, because of their beautiful flowers, are the two endemic species of *Gardenia*. The blossoms are large, white, deliciously fragrant, and rank high among the wild flowers of Hawaii. The coffee (*C. arabica*) was introduced in 1823, and its cultivation spread rapidly to all of the larger islands of the group. Although a combination of economic and cultural factors has largely suppressed the coffee industry, the plant itself is thoroughly naturalized, and occurs in many of the humid lower regions. Birds have undoubtedly assisted in its dissemination.

Rutaceae

Rutaceous trees and shrubs comprise a conspicuous and abundant element in the native forests. There are few groves or wooded slopes that do not contain a generous proportion of rutaceous

²¹ The algaroba or mesquite (*Prosopis juliflora*) was introduced nearly a century ago, and has become widely spread through the agency of cattle. Today it is one of Hawaii's most valuable trees, and is abundant on the lowlands to the 2000 foot contour. It is an important source of honey, nutritious pods, and firewood, and greatly ameliorates the soil upon which it grows.

species. Two of the three genera (*Pelea* and *Platydesma*) are endemic; the third (*Zanthoxylum*) is world wide in its range. *Pelea*, named in honor of the Hawaiian volcano goddess Pele, is a large genus, with nearly 30 recognized species and an even larger number of varieties. Like the species of *Cyrtandra* and the lobeliaceous genera, the species of *Pelea* are highly variable, with many intergrading forms, so that as yet the species are poorly defined.

Platydesma is an isolated genus, with 4 woody species. *Zanthoxylum* has 7 species, 6 arborescent, and many varieties. The majority of these are characteristic of arid leeward regions and old lava flows. There are no native citrus fruits, although the orange has become naturalized in many districts, particularly in the Kona district, on Hawaii.

Violaceae

The endemic Violaceae are a distinct surprise to the mainland botanist on his first excursions in our Hawaiian forests. Instead of tender little herbs, he finds stout woody shrubs, ranging in height from 3 to 6 ft. The flowers are quite like those of the familiar eastern violets, and are white, pink, purple, or blue in color, according to species. There are 7 or 8 species, ranging in habitat from hot, exposed, semiarid regions to the cold, rain-soaked summit bogs. They occur on all the islands, and in certain favorable localities, as the Molekai swamps, they cover considerable areas.

Several species, for example *V. helioscopia*, have large showy flowers of great beauty and fragrance, and suggest novel horticultural possibilities in the way of cultivated violet bushes. Undoubtedly, as familiarity with the native flora increases and methods for transplanting and culture are improved, some of these lovely shrubs will be utilized in horticulture.

Araliaceae

This large and widely distributed family is prominent in the Hawaiian flora. All of our species are trees, and many of them form a conspicuous feature of the xerophytic woodlands, inhabiting the barren lava fields and other arid regions. The Araliaceae had two great centers of distribution, tropical America and Malaya.

It is probable that Hawaii originally received its contribution from the Malayan center, although its 4 genera are now almost wholly endemic.

All of the 13 or more Hawaiian species are endemic, and of these a number are sharply localized in their range. The 4 genera are represented as follows: *Tetraplasandra*, 7 spp.; *Reynoldsia*, 1 sp.; *Pterotropia*, 3 spp.; *Cheirodendron*, 2 spp. The characteristic American-Asiatic genera *Aralia* and *Panax* do not occur in Hawaii.

Labiatae

The Labiatae are represented by 7 genera. Three (*Stenogyne* with 16 to 18 species, *Phyllostegia* with about 20 species, and *Haplostachys* with 3 species) are endemic. *Plectranthus* comes from Australia, and *Sphacele* from the Pacific Coast of America. The two remaining genera (*Salvia* and *Stachys*) are weeds of world-wide geographic range.

Hawaii has no equivalent for the familiar mints of eastern fields and waysides, such as catnip, peppermint, pennyroyal, hoarhound, and a score of others. Our *Sphacele hastata*, endemic from an Andean genus, is a typical example of precinctiveness. It forms an extensive belt around the great volcanic mountain Hale-a-ka-la at an elevation of about 3000 ft., and occurs nowhere else in the archipelago.

Many of the shrubby species of *Phyllostegia* and *Stenogyne* have lovely masses of flowers, white, pink, and red, and give beautiful color effects against the dark greens of the rain forest and the wet shadowy jungles which they inhabit.²²

Malvaceae

The Malvaceae constitute a large family, dispersed over the whole world, except the arctic regions, and richly represented in the tropics and subtropics. Hawaii is well endowed with this group. There are 2 endemic genera: *Kokia*, the Hawaiian tree cotton, with 2 species; and *Hibiscadelphus*, with 3 species. All of these are excessively rare and localized.

²² MACCAUGHEY, V., The wild flowers of Hawaii. Amer. Bot. 22:97-105, 131-135. 1916.

The large genus *Hibiscus* has 6 or 7 native species, all shrubs or trees, with large flowers of striking beauty. The blossoms are white, pink, red, or yellow, according to species, and form a distinctive feature of the rain forest.

The cosmopolitan genera *Malva*, *Malvastrum*, *Sida*, and *Abutilon* are common on the semiarid lowlands. *Gossypium*, the true cotton, includes the unique Hawaiian cotton, *G. tomentosum*, a spreading shrub, endemic, densely covered with white tomentum, and growing in arid situations along the coasts.

Solanaceae

Of the 70 genera of this family, only 3 (*Solanum*, *Nothocestrum*, and *Lycium*) comprise elements in our native flora. There are many introduced Solanaceae (*Physalis*, *Datura*, *Nicotiana*, etc.), some brought in at a very early period and now thoroughly established. The genus *Solanum* has 6 endemic species, one arborescent; in addition to these there are a number of weeds belonging to this genus. *Nothocestrum* is an endemic genus of 4 arborescent species, and is closely related to the Brazilian genus *Athenaea*. *Lycium*, a genus of 70 species, is represented in our flora by a single widely distributed littoral species.

Grasses

The grasses, including many introduced and now naturalized species, have about 40 genera in the flora. None of these are endemic, although there are a number of endemic species. Some of the more important genera, from the standpoint of distribution and number of species, are *Bromus*, *Calamagrostis*, *Cenchrus*, *Chloris*, *Chrysopogon*, *Cynodon*, *Dactylis*, *Eleusine*, *Eragrostis*, *Festuca*, *Heteropogon*, *Holcus*, *Koeleria*, *Lolium*, *Panicum*, *Paspalum*, *Poa*, and *Stenotaphrum*.

The highly developed sugar-cane industry has monopolized most of the arable lowlands, and needs no further comment here. Rice and corn are also raised; in early times wheat, barley, and oats were exported to California, but are now imported. Clumps of *Bambusa vulgaris*, early naturalized, are scattered here and there in the humid valleys. The prevalent lawn grass in Hawaii is the Bermuda grass, *Cynodon dactylon*.

The representation of Cyperaceae is roughly as follows: *Cyperus* 17 spp., *Kyllingia* 1, *Fimbristylis* 4, *Eleocharis* 1, *Scirpus* 2, *Hypolytrum* 1, *Rhynchospora* 4, *Cladium* 1, *Baumea* 1, *Vincentia* 1, *Gahnia* 5, *Oreobolus* 1, *Scleria* 1, *Uncinia* 1, *Carex* 5.

Absent pests

Hawaii is entirely free from any plants poisonous to the touch. To the botanist familiar with the distressing prevalence of these pernicious vines and shrubs in the continental woodlands, it is a relief to work one's way through a Hawaiian jungle with the certainty of complete safety in this regard. Neither are there any stinging nettles. *Mucuna urens*, the well known "cow-itch" plant, whose pods are covered with stinging hairs, is naturalized in certain restricted areas on the islands of Maui and Hawaii.

The Anacardiaceae are represented in Hawaii by a single arborescent Asiatic *Rhus* (*R. semialata* Murray var. *sandwicensis* Engler). This species extends from India and the Orient to Hawaii, and is non-poisonous. Our variety is a small tree, growing in isolated clumps in all the islands.

It is to be hoped that the pernicious *T. vernix*, *T. radicans*, and *T. Toxicodendron* of North America may never by any accident reach Hawaii. The noisome *Paederia foetida* was accidentally introduced a number of years ago, and its seeds, like those of *Rhus Toxicodendron*, are abundantly distributed by birds. It is now a pest in many of the valleys, as it smothers all other vegetation.

Ferns

There are 43 genera and 185 species of pteridophytes; of these, 2 genera and 118 species are endemic. There are 18 genera with all or 75 per cent and over of endemic species; 18 genera possess no endemic species, or have 75 per cent or over of non-endemic species; 33 species are practically cosmopolitan; 8 species have the west coast of America as their chief station; 22 species have the South Pacific as their chief station; and 2 species have the east coast of Asia as their homeland.

The fern flora of Hawaii is rich and diversified. Like the lichens and the mosses, the ferns are to be found in all habitats,

from the arid raw lava flows to the most humid portions of the jungle forest. A number of species (*Cibotium* and *Sadleria*) attain arborescent stature (8–35 ft.) and many others are of large size.²³ The other extreme is found in the minute Hymenophyllaceae. These are abundant in the rain forest, and clothe the trees with their filmy fronds.

There are about 22 genera of true ferns. The largest of these are *Asplenium*, 40 spp.; *Dryopteris*, 21; *Polypodium* 14, *Elaphoglossum* 8, *Diellia* and *Athyrium* 6, *Sadleria* 5, *Trichomanes* 4. The number of species in the larger genera, and in some of the smaller as well, must be stated as approximations, as many of these species are in serious need of revision. Many of the forms hitherto described as varieties will undoubtedly be raised to specific rank upon careful investigation, and numerous specific descriptions require redefinition.

Some of the abundant forms not indicated by the generic list are *Marattia Douglasii*, *Gleichenia* spp., *Gymnogramme javanica*, *Vittaria elongata*, *Nephrolepis exaltata*, *Cystopteris Douglasii*, *Doodya media*, *Odontoloma repens*, *Micropelia* spp., *Schizostegia Lydgatei*, *Pellaea ternifolia*, and *Adiantum* spp. These are all of genera represented by only a few species.

Salviniaceae are represented by a recently introduced *Azolla*; Marsileaceae by 2 endemic species of *Marsilea*; Equisetales are not represented. The Lycopodiales have 3 genera in the flora: *Lycopodium* with 10 spp. and 5 endemic; *Psilotum* with 20 widely distributed species; and *Selaginella* with 3 endemic and 1 other species. About 50 of the Hawaiian pteridophytes are epidendrous; 15 are xerophytic; and about 15 are lithophilous. The great majority inhabit the rain forests at elevations of 1000–6000 ft.

Bryophytes

Mosses are also very abundant, both in dry and humid regions. In the rain forest are many epiphytic species that clothe the trunks and branches with a dense, soggy envelope of greenery. These jungle moss forests are very beautiful. The summit bogs are the

²³ MACCAUGHEY, V., The tree ferns of Hawaii. Amer. Bot. 22:1–9. 1916.

habitats of many mosses, which completely cover the water-saturated ground of large areas, and mask the treacherous quagmire.²⁴ The liverworts, including the Marchantiales, Anthocerotales, and Jungermanniales, are abundant in the humid regions, many species being epiphytic and epiphyllous. Species of *Marchantia*, *Anthoceros*, and related genera are conspicuous along streamways and in other moist places.

Fungi

The larger fungi are conspicuously absent from the woodlands. There are a few woody brackets, a few dull-colored mushrooms, a few puffballs and trembling fungi. The sum total of all these is insignificant, however, when compared with the rich fungus flora of such a region as the eastern United States. One may gather more fleshy fungi in a day's collecting in New York, for example, than he would find in diligently scouring our forests for a week. This condition is somewhat surprising, as the cool, humid rain forest zone, with its abundance of decaying vegetation, would appear to be favorable for the development of the fleshy fungi. A number of species of slime molds occur in the ravines and jungles. It is to be regretted that no comprehensive study of the Hawaiian fungi has been made.²⁵

Lichens are abundant in all parts of the islands. They comprise the first invaders of the freshly cooled lava flows. They luxuriate in the cool humidity of the rain forest and the summit bogs. They cover the exposed cliffs and ledges of the middle zones, and withstand the aridity of the leeward lowlands and of the high mountains (6000-14,000 ft.). The lichen flora not only occupies a wide variety of ecological areas, but furthermore is of considerable richness. No comprehensive statement can be made as to genera and species, as the Hawaiian lichens have never received exhaustive study.

²⁴ GATES, F. C., A sphagnum bog in the tropics. *Jour. Ecology* 3; 24-30. *pl. 1. fig. 1.* 1915.

²⁵ RICHARDS, H. W., *Beiträge zur Flora der Hawaiischen Inseln.* Vienna. 1878.

BERKELEY, M. J., Description of fungi collected by R. B. HINDS in islands of Pacific. *Hook. Jour.* 1842.

———, Fungi of the Challenger Expedition. *Linn. Jour.* 1878.

Aboriginal introductions

Any outline of the Hawaiian flora would be seriously defective that did not give prominence to the numerous plant introductions by the primitive Hawaiians in their migrations from Samoa and the South Seas. Carefully gathered historical evidence has established the fact that during a long period of time, probably several centuries, the ancient Hawaiians maintained intercourse with their kinfolk in the South Pacific, making the long voyages in their splendid canoes. During this eventful period of migration and intercourse with the south, about 25 species of useful plants were consciously introduced by the natives, and perhaps a much larger number unconsciously brought in as seeds and spores. The list includes:²⁶

- **Colocasia esculenta*; the taro; starchy corms used for food.
- Ipomoea Batatas*; sweet potato; many native varieties.
- **Musa sapientum* banana; many native varieties.
- Artocarpus incisa*; breadfruit tree; seedless.
- **Cocos nucifera*; cocoanut palm; formerly very common.
- **Dioscorea sativa*; yam; starchy tubers; climbing vine.
- **Dioscorea pentaphylla*; yam; starchy tubers; climbing vine.
- **Alocasia macrorrhiza*; giant taro; starchy corms.
- **Tacca pinnatifida*; arrowroot; starchy rhizomes.
- **Jambosa malaccensis*; mountain apple tree; delicious fruits.
- Saccharum officinarum*; sugar cane; several native varieties.
- **Cordyline terminalis*; ti bush, with sweet, edible roots.
- **Piper methysticum*; awa vine; famous Polynesian intoxicant.
- **Zingiber Zerumbet*; wild ginger; common in lower forest.
- **Curcuma longa*; well known dye plant; yellow rhizomes.
- **Aleurites moluccana*; kukui or candlenut tree; illuminating oil.
- **Calophyllum Inophyllum*; kamani tree; shade, wood, and oil.
- **Hibiscus tilaceus*; hau tree; fiber, wood, and shade.
- **Pandanus odoratissimus*; hala tree; fiber and food.
- **Broussonettia papyrifera*; wauke bush; cloth plant of Polynesia.
- **Boehmeria stipularis*; opuhi bush; fiber plant.
- **Thespesia populnea*; milo tree; shade and wood.
- **Cordia subcordata*; kou tree; shade and wood.
- Cucurbita maxima*; large gourd, for calabashes.
- Lagenaria vulgaris*; small gourd, for calabashes.

²⁶ MACCAUGHEY, V., The food plants of the ancient Hawaiians. *Sci. Monthly* 4:75-80. 1917.

The starred names indicate species that have escaped from cultivation. Many of these have become so thoroughly naturalized and established in the lower forests, on the lowlands, and along the beaches that they are easily confused with the true indigenous flora.

The successful importation of this diversified series of edible, fiber-producing, oil-producing, and other useful plants, from lands so remote, and by methods so primitive, betokens native horticultural skill of no mean importance. As stated by LYDGATE, "the successful introduction, perhaps acclimatization even, must have meant repeated voyages, extending over generations or even centuries. And not time alone, but patience and skill must have been required for the successful introduction of a seedless tree like the breadfruit. Under favorable conditions it is not easy to propagate; exposed to the trying vicissitudes of a long canoe voyage, weeks of wind and weather and open sea, lack of water, burning sun and blighting spray, huddled into the bottom of the shallow canoe, how many, many failures there must have been."

In conclusion, it may be pertinent to suggest that there is an unwritten chapter in the history of Hawaii's introduced flora, namely the introductions possibly made by the early Spanish explorers. They undoubtedly visited the islands repeatedly, long before the discovery by COOK²⁷; there are numerous evidences of their intercourse with the natives, and it is not all beyond the realm of probability that some of the plants now thoroughly naturalized were brought in by these early Spaniards.

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²⁷ Historical evidence shows that probably the first Europeans to land on the Hawaiian Islands were shipwrecked Spaniards, in November, 1527. In 1555 they were discovered by the Spanish navigator JUAN GAETANO, over 200 years before the famous discovery by Captain JAMES COOK (1778).